CHICK GROWTH AND PROVISIONING OF SURVIVING AND NONSURVIVING WHITE-TAILED TROPICBIRDS (*PHAETHON LEPTURUS*)

JAIME A. RAMOS[1,2] AND CARLOS PACHECO[1]

ABSTRACT.—We examined variation in meal size, feeding frequency and daily food delivery in relation to age, nest, day, year, and weather by White-tailed Tropicbirds (*Phaethon lepturus*) using repeated weighing of chicks. We focused particularly on the differences between chicks which survived and those which died. Unsuccessful chicks became significantly lighter than successful chicks at the age of 30 days; however, some were fed until they were 60 days old. Feeding frequency and meal size differed significantly between both age classes and between surviving and nonsurviving chicks. In surviving chicks, feeding frequency remained relatively constant until chicks reached 60 days and dropped progressively thereafter. In this group, meal size was significantly lower in chicks up to 20 days old and over 70 days old than those aged 21–70 days. We found significant relationships between chick food provisioning and day, nest, and year. Feeding frequency was more important than meal size in explaining the difference in food delivery between surviving and nonsurviving chicks. This was due to much greater significant differences for feeding frequency than for meal size between surviving and nonsurviving chicks, including annual differences in feeding frequency (but not in meal size) for surviving chicks. Our study suggests that parents of unsuccessful chicks had difficulty in obtaining sufficient food for their chicks from very early on, but responded to this problem first by decreasing the feeding frequency and, later, decreasing both feeding frequency and meal size. Our study shows that parents vary in their abilities to provide optimal provisioning to their chicks. Environmental conditions determine further energetic constraints in food delivery to chicks. *Received 16 May 2003, accepted 10 October 2003.*

Pelagic seabirds are characterized by low reproductive rates, great longevity, and long incubation and chick-rearing periods, and their chicks exhibit relatively low growth rates (Ashmole 1963, Lack 1966, Warham 1990). Studies of chick provisioning in pelagic seabirds have been conducted mostly on procellariiforms and sphenisciforms in temperate and polar regions, respectively (Huin et al. 2000, Phillips and Hamer 2000 and references within). Apart from the studies of Schaffner (1990) and Schreiber (1994, 1996) on tropicbirds (*Phaethon* spp.), tropical species have received less attention, especially in describing the pattern of food delivery to chicks of all ages.

Breeding failures of entire colonies, uncommon in temperate areas (but see Schreiber 2002), occur regularly in the tropics (Ashmole 1963, Ramos et al. 2002). White-tailed Tropicbirds (*Phaethon lepturus*) have an exclusively tropical and subtropical distribution, have greater feeding frequencies (despite great variability, adults feed their chicks daily; Schaffner 1990), and show a lower productivity (0.20–0.46 chicks/breeding pair; Stonehouse 1962, Prys-Jones and Peet 1980, Phillips 1987) than other tropical seabirds, such as the Red-tailed Tropicbird (*P. rubricauda*; Schreiber 1994), and other pelagic seabirds such as the Procellariiformes (Warham 1990). These characteristics make White-tailed Tropicbirds a good subject to address the importance of feeding frequency versus meal size in the success of a nest. On Aride Island, Seychelles, where this study was conducted, the White-tailed Tropicbird breeding population has shown a 60% decrease since 1988 (Bowler et al. 2002); therefore, it is important to examine whether anomalies in chick food provisioning correlate with this decline.

We used repeated weighing of chicks to investigate temporal patterns in chick provisioning by White-tailed Tropicbirds throughout the period of nestling development. We investigated daily variation in (a) meal size (amount of food delivered by one or both parents on days that chicks were fed), (b) feeding frequency (proportion of days that chicks were fed), and (c) daily food delivery (amount of food received per day, including the value zero for days when no food was received) in relation to chick age, survivorship class (surviving versus nonsurviving chicks), nest, day,

[1] Inst. of Marine Research, Dep. de Zoologia, Univ. de Coimbra, 3004–517 Coimbra, Portugal.

[2] Corresponding author; e-mail: jramos@ci.uc.pt

year, and wind speed. We examined whether meal size, feeding frequency and daily food delivery were similar among nests. The primary objective of our study was to describe seasonal and annual variations in meal size, feeding frequency, and daily food delivery of surviving and nonsurviving White-tailed Tropicbird chicks. We then discuss these parameters in relation to foraging strategies of seabirds, in particular the relationships of feeding frequency and meal size to nest success, and the influences of temperate and tropical environments.

METHODS

We studied White-tailed Tropicbirds between 2 June and 31 September of 2001 and 2002 on Aride Island, Seychelles (4° 10′ S, 55° 40′ E). We marked nests with eggs and chicks of different ages during daily routine walks along the plateau and part of the adjacent hill in June and July of 2001 and 2002. Parents brood their chicks for about 5 days after hatching and a repeated weighing protocol began when chicks were no longer being attended continuously. We obtained the weights and wing chords of a group of 10–15 chicks of known age daily at 06:00 (UTC + 4 h) during 2001. The other chicks were aged from wing length calibrated against growth of the chicks of known age. During 2002 we marked nests with chicks aged 21–65 days. We weighed 11–25 chicks every day between 2 June and 1 August, 2001 (except on 17, 22, 24, 26, 29 and 30 July), and 5–25 June 2002. We used the larger data set of 2001 in all comparisons between surviving and nonsurviving chicks. Data for 2002 was used only to compare chick food provisioning between 2001 and 2002, for surviving chicks aged 21–70 days.

In 2001, 12 chicks were weighed at 6-h intervals (06:00, 12:00, 18:00 and 00:00) during the first five days of the study. However, since only a small increment in body mass (3–7 g) was detected between 18:00 and 00:00, and that was for only three chicks <11 days old (5% of the chick days), no further chicks were weighed at 00:00 after 6 June. Schreiber (1994) also showed that Red-tailed Tropicbirds are not fed at night. Any overnight gains in body mass were omitted from the analyses. In August and September all remaining chicks

were checked once or twice a week to assess whether they survived or not.

Daily feeding events were determined from the repeated weighings. Each weighing period lasted 30–40 min and chicks were always weighed in the same sequence. On six occasions chicks regurgitated food while being handled, but this was fed back to the chicks. Increases in chick mass between weighings were attributed to feeding by adults, and positive mass increments were used to estimate meal sizes, feeding frequency, and daily food delivery following established procedures (Ricklefs et al. 1985, Bolton 1995, Phillips and Hamer 2000). The sums of positive mass increments (SUM; Ricklefs 1984) between repeated 6-h weighings each day are an index of the amount of food delivered by the parents. This underestimates the amount of food delivered because chicks loose mass through respiration and excretion over this period. We estimated mass loss before and after feeding in 2001, using stepwise multiple regression (Bolton 1995, Phillips and Hamer 2000). Stepwise multiple regression was used to investigate the relationship between rates of mass loss by chicks, in the intervals before feeding and after feeding, and initial mass, chick age, and the size of meal received. The best predictions were obtained with untransformed data. The rate of mass loss prior to a feeding was significantly and independently related to both initial mass and chick age. Initial mass (g) accounted for 14.6% of the variation in mass loss (g/h) and chick age (days) accounted for 13.4%: mass loss = 0.012 (± 0.001 SE) × initial mass − 0.033 (± 0.005 SE) × age − 0.051 (± 0.212 SE); $F_{2,234}$ = 46.4, r^2 = 0.28, P < 0.0001. The rate of mass loss following a feeding was significantly and independently related to initial mass, amount of food received, and chick age, which accounted for 55%, 11% and 1% of the variation, respectively: mass loss = 0.011 (± 0.001 SE) × initial mass − 0.018 (± 0.002 SE) × meal size − 0.013 (± 0.004 SE) − 0.614 (± 0.176 SE); $F_{3,307}$ = 210.2, r^2 = 0.67, P < 0.0001.

We used the above equations to estimate mass loss between initial and final consecutive weighing periods, assuming that the feedings occurred in the middle of the weighing period. This estimate was then used to correct SUM,

in order to determine the total amount of food delivered to the chick. The correction was applied when a positive increase in mass was detected between weighings. Therefore, very small meals delivered soon after one weighing may have been undetected, but these would be of low energetic value to the chick.

Meal size represents the amount of food, given by one or both parents, delivered on days that chicks were fed. We stress that our definition of meal size is not coincident with meals of individual parents, as measured in previous studies of White-tailed Tropicbirds (Schaffner 1990). We defined daily food delivery as the total amount of food received on a daily basis; the value zero was used for days when no food was received. We assessed the relationship of total daily food delivery, chick age, and chick mass at 06:00 on the 24-h mass changes of chicks from 06:00 to the following 06:00 (NET; Ricklefs 1984).

The weighing data represented repeated measurements from the same chicks. All analyses were done separately for surviving and nonsurviving chicks. Data on estimated meal size and estimated daily food delivery were normalized by log (x) and log ($x + 1$) transformation, respectively. However, for surviving chicks, results obtained with transformed and untransformed data were very similar, possibly due to the larger sample size. As the sample size for nonsurviving chicks was smaller we performed all analyses on transformed data.

We examined differences in feeding frequency among age classes with Kruskal-Wallis nonparametric analysis of variance. We used logistic regression to evaluate the relationship between chick feeding frequency (fed, not fed) and day and nest. The dependence of meal size and daily food delivery from age class, day, nest, and year was examined with one-way ANOVA. When significant differences were found, *post hoc* tests were conducted using the Tukey test (Zar 1996). For 2001, we also examined the relationship between wind speed and mean daily food delivery for surviving chicks using the Pearson correlation coefficient. We obtained daily mean wind speed for the period June to July 2001 (in knots; 1 knot = 1.85 km/h) from the meteorological station at Mahé airport, about 40 km from Aride. We assumed that
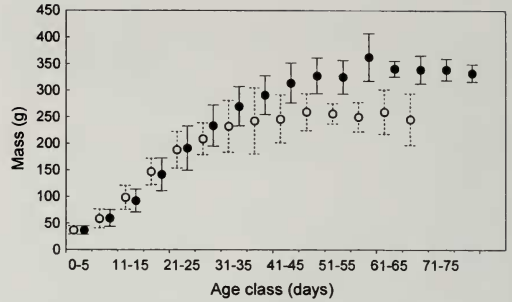

FIG. 1.   Growth curves (mean ± SD) for surviving (closed circles) and nonsurviving (open circles) White-tailed Tropicbird chicks on Aride Island, Seychelles, in June and July 2001. The number of chick-days for each age class ranged from 8–106; median = 41 for surviving chicks and 13 for nonsurviving chicks.

these values represent the mean wind speed conditions in the area of inner Seychelles where White-tailed Tropicbirds foraged.

To test whether weighing chicks at intervals throughout the day might disturb feeding events, we compared body mass of chicks weighed at 6-h intervals to those of 10 chicks weighed once a day at 06:00, over the same period in 2001. These extra 10 chicks were interspaced with the other chicks; therefore, the 06:00 round lasted up to 55 min.

RESULTS

Chick growth.—There was no significant difference in age specific masses of frequently weighed chicks compared to chicks weighed only once a day in 2001 (ANCOVA with age as covariate, $F_{1,1768} = 0.37$, $P = 0.30$).

Changes in body mass of surviving and nonsurviving chicks in 2001 in relation to chick age are presented in Fig. 1. Chicks that survived reached a mean peak mass of 362.4 g ± 44.7 SD at the age class of 56–60 days. Mass of chicks that did not survive was similar to that of surviving chicks until 21–25 days, but thereafter the difference between the two groups increased with age (Fig. 1). Surviving chicks increased in mass at a mean rate of 7.8 g/day from hatching until 35 days, and growth slowed to 3.7 g/day from 36–60 days. From 61–80 days chicks lost mass at a mean rate of 1.5 g/day. Nonsurviving chicks gained mass at a similar rate to that of surviving chicks (mean of 7.6 g/day) until 25 days, but their growth slowed to a mean of 2.5 g/day from 26–50 days. Nonsurviving chicks lost

TABLE 1. Feeding frequency (proportion of days that chicks were fed) and meal size (amount of food delivered by one or both parents, delivered on days that chicks were fed) for surviving and nonsurviving White-tailed Tropicbird chicks on Aride Island, Seychelles, in June and July 2001. Values are mean ± SD, n = number of chick-days.

Age class (days)	Feeding frequency				Meal size (g)			
	Surviving	n	Nonsurviving	n	Surviving	n	Nonsurviving	n
<10	1.00 ± 0.0[a]	16	0.86 ± 0.36[a]	21	26.9 ± 19.6[a]	16	26.0 ± 10.7[a]	18
11–20	0.96 ± 0.21[a]	90	0.88 ± 0.33[a]	50	51.0 ± 22.5[a]	86	43.8 ± 18.8[ac]	44
21–30	0.89 ± 0.32[a]	116	0.75 ± 0.43[b]	57	69.3 ± 30.4[a]	103	65.1 ± 26.7[a]	43
31–40	0.96 ± 0.93[a]	134	0.78 ± 0.42[a]	46	71.9 ± 32.8[a]	118	66.8 ± 30.2[a]	36
41–50	0.92 ± 0.27[a]	125	0.71 ± 0.46[b]	49	75.6 ± 33.3[a]	115	60.1 ± 26.4[b]	35
51–60	0.92 ± 0.27[a]	117	0.72 ± 0.45[b]	36	74.9 ± 32.4[a]	108	57.6 ± 27.0[b]	26
61–70	0.80 ± 0.40[a]	85	0.45 ± 0.51[b]	20	76.3 ± 32.1[a]	68	64.9 ± 26.1[a]	9
71–80	0.73 ± 0.45	37			54.2 ± 27.4	27		

[a,b] For each group, feeding frequency and meal size, rows sharing the same letter were not significantly different (Kruskal-Wallis and t-tests comparing chicks of the same age class for feeding frequency and meal size, respectively).
[c] The difference was not significant when two outliers of the surviving group were removed.

mass at a mean rate of 0.6 g/day from 51–70 days.

Feeding frequency.—The proportion of surviving chicks in 2001 that were fed each day was higher at all age classes than that of nonsurviving chicks (Table 1). The feeding frequency for surviving chicks remained relatively constant until chicks reached 60 days and decreased progressively thereafter. There were significant differences in the probability of surviving (Kruskal-Wallis $H_{7,720}$ = 24.8, P = 0.007) and nonsurviving ($H_{6,279}$ = 16.3, P = 0.012) chicks being fed according to age class (Table 1). For surviving chicks, those in the older age classes (>60 days) were fed less frequently than younger chicks (Table 1). For nonsurviving chicks, feeding frequency was significantly higher in chicks aged up to 20 days than for those aged 21–60 days, and higher in both these groups than in chicks aged 61–70 days. Kruskal-Wallis pairwise comparisons for each age class showed that feeding frequency differed significantly between surviving and nonsurviving chicks for all age classes over 20 days, except those aged 31–40 days (Table 1).

For chicks aged 21–70 days in 2001, there was no significant relationship between chick feeding frequency (fed, not fed) and day and nest, for both surviving (logistic regression Wald χ^2_1 = 2.70, P = 0.26) and nonsurviving chicks (χ^2_1 = 4.24, P = 0.12). For surviving chicks aged 21–70 days, the daily feeding frequency in 2001 was significantly higher than that in 2002 (Table 2). Overall, chicks were fed significantly more in the morning than in the afternoon during both 2001 and 2002 (58.2% and 60.1% of the feedings in the morning, respectively; χ^2_1 = 29.2, P < 0.0001, n = 1087, and χ^2_1 = 6.7, P = 0.008, n = 173).

Meal size.—In 2001, meal size in the surviving group was significantly lower in chicks aged up to 20 days and over 70 days than

TABLE 2. Feeding frequency (proportion of days that chicks were fed), meal size (amount of food delivered by one or both parents, delivered on days that chicks were fed) and daily food delivery (total amount of food received on a daily basis; the value zero was used for days when no food was received) for surviving White-tailed Tropicbird chicks, aged 21–70 days. Values are mean ± SD, n = number of chick-days. Data are from Aride Island, Seychelles.

	2001		2002		Statistic	
Feeding frequency	0.89 ± 0.31	(n = 577)	0.80 ± 0.40	(n = 181)	χ^2_1	= 8.6, P = 0.003
Meal size (g)	73.6 ± 32.1	(n = 511)	74.4 ± 31.0	(n = 145)	$F_{1,654}$	= 0.68, P = 0.410
Food delivery (g)	65.3 ± 38.1	(n = 577)	59.3 ± 40.8	(n = 182)	$F_{1,757}$	= 8.23, P = 0.004
Daily mass increments (NET, g)	3.25 ± 20.3	(n = 705)	0.81 ± 19.8	(n = 182)	$H_{1,885}$	= 1.46, P = 0.230

those aged 21–70 days, but no significant difference was detected between chicks aged 11–20 and those aged 71–80 (one-way ANOVA $F_{7,632} = 16.6$, $P < 0.0001$). In 2001, meal size for nonsurviving chicks also differed significantly among age classes (one-way ANOVA $F_{6,205} = 10.2$, $P < 0.0001$). Meal size for chicks aged up to 10 days was significantly lower than in all other chicks, and meal size for chicks aged 11–20 was significantly lower than those aged 21–40 days (Table 1). Paired *t*-tests between surviving and nonsurviving chicks of each age class showed that meal size differed significantly only for chicks aged over 41 days (Table 1).

The dependence of meal size on nest was used to assess consistency in the size of meals delivered to surviving chicks aged 21–70 days (for which meal size was independent of age). This analysis showed a significant degree of variation between chicks in meal size received in 2001 ($F_{18,492} = 2.60$, $P = 0.0004$) but not in 2002 ($F_{11,133} = 1.28$, $P = 0.24$). From 18 nests in 2001, one nest (mean = 50.4 g) was different from two other nests (mean = 87.3 and 85.9). For the same age group, daily variation in meal size was significantly different in 2001 ($F_{54,456} = 1.67$, $P = 0.003$) but not in 2002 ($F_{18,126} = 1.57$, $P = 0.082$. Tukey range tests identified a significant difference between 4 July (meal size = 47.1 g) and 23 and 26 July 2001 (meal sizes of 97.3 and 93.8 g, respectively). For surviving chicks aged 21–70 days meal size did not differ significantly between 2001 and 2002 (Table 2).

For nonsurviving chicks in 2001, there was a significant association between nest and meal size ($F_{9,178} = 2.74$, $P < 0.005$), but no significant differences were found with Tukey tests. No significant association was obtained between day and meal size ($F_{52,87} = 0.87$, $P = 0.071$).

Total daily food delivery.—The mean amount of food received each day in 2001 for surviving and nonsurviving chicks in each age class is shown in Fig. 2. For surviving chicks, daily food delivery for chicks aged 11–60 differed significantly from chicks aged 71–80 ($F_{7,712} = 3.61$, $P = 0.0008$). There was no significant difference in daily food delivery among age classes for nonsurviving chicks ($F_{6,272} = 1.94$, $P = 0.074$).
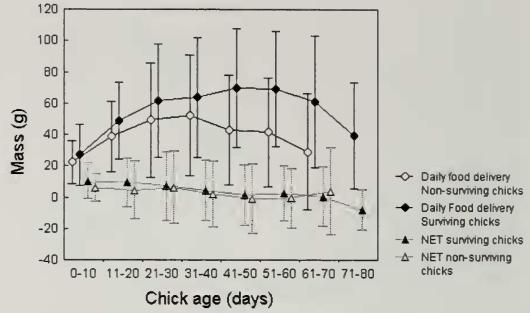
For surviving chicks aged 20–70 days, total

FIG. 2. Estimated daily food delivery and 24-h mass change (NET; mean ± SD) in relation to chick age for surviving and nonsurviving White-tailed Tropicbird chicks on Aride Island, Seychelles, in June and July 2001 ($n = 37$–134 surviving chicks and 20–57 nonsurviving chicks).

daily food delivery differed significantly among chicks ($F_{18,558} = 2.66$, $P = 0.0002$) and days ($F_{54,522} = 1.89$, $P = 0.0003$) in 2001. Two chicks (mean food delivered = 40.6 and 44.6 g) differed from seven other chicks (mean food delivered = 60.6–83.2 g). In terms of daily variation, there was a significant difference between 5 July 2001 (mean food delivered = 33.1 g) and 18 and 23 July 2001 (mean food delivered = 91.8 and 97.3 g, respectively). In 2002, total daily food delivery differed significantly among days ($F_{18,163} = 1.90$, $P = 0.020$, although no significant differences were found with the Tukey test) but not among nests ($F_{11,170} = 1.06$, $P = 0.15$).

There also was a significant relationship between nest and overall food delivery of nonsurviving chicks in 2001 ($F_{10,199} = 1.95$, $P = 0.041$). The Tukey test identified a difference between one nest (mean food delivered = 30.3 g and two others (mean food delivered = 62.8 and 63.5 g). For surviving chicks aged 21–70 days, total daily food delivery differed significantly between 2001 and 2002 (Table 2).

There was no significant correlation between mean daily food delivery and wind speed for surviving chicks aged 20–70 days in 2001 ($r = -0.19$, $P = 0.20$, $n = 54$). The relationship of day and wind speed with total daily food delivered for nonsurviving chicks was not examined due to a small sample size for each day.

Daily mass change.—Changes in daily mass increments (NET) for surviving and

nonsurviving chicks in 2001 are presented in Fig. 2. In a stepwise multiple regression, NET (in g) was significantly and independently related to daily food delivery, age, and chick mass at 06:00 according to the following equation (for both surviving and nonsurviving chicks, since equations were similar for each group): NET = 4.89 ($\pm$ 0.97 SE) + 0.47 ($\pm$ 0.009 SE) $\times$ daily food delivery + 0.27 ($\pm$ 0.03 SE) $\times$ age $-$ 0.16 ($\pm$ 0.006 SE) $\times$ mass at 06:00 ($F_{3,900}$ = 1059.0, P < 0.0001, r^2 = 0.78).

Variation in daily food delivery accounted for 56% of the variation in NET and, after controlling for that, NET was greater in older chicks and lower in chicks that were initially heavier. Mean daily mass increments for surviving chicks aged 21–70 days did not vary significantly between 2001 and 2002 (Table 2).

DISCUSSION

Pattern of chick provisioning for surviving and nonsurviving chicks.—It is not surprising that chicks that died experienced a low provisioning rate that ultimately resulted in starvation and death. Feeding frequency was more important than meal size in explaining the difference in chick food delivery between surviving and nonsurviving chicks, because there were much greater differences for feeding frequency than for meal size between surviving and nonsurviving chicks. Moreover, surviving chicks showed a significant difference in feeding frequency (but not in meal size) between years. Our study shows that significantly lower feeding frequency of nonsurviving chicks occurred from the age of 20 days onwards, whereas significantly lower meal size occurred only from the age of 41 days. This means that parents of unsuccessful chicks had difficulties in finding and catching the necessary food for their chicks from very early on but responded to this problem first by decreasing the feeding frequency and later, by decreasing both feeding frequency and meal size. Thus, a reduction in the rate of increase in mass was apparent from about day 30. We found that (1) within each year nonsurviving chicks had lower performing parents, and (2) parents of surviving chicks showed a significant difference in performance between years.

In terms of the time of day that food was delivered to chicks, 58% of the feedings on

Aride were before 12:00; in contrast Schaffner (1990) recorded about 90% of the meals in Puerto Rico before 12:00. Schreiber (1994) also found that 71–73% of adult feedings in Red-tailed Tropicbirds breeding on Christmas Island and Johnston Atoll, central Pacific Ocean, were delivered between 07:00 and 13:00. The fact that White-tailed Tropicbird chicks were more likely to be fed in the morning than in the afternoon at both Aride and Puerto Rico suggests that nocturnal feeding on species such as squid, which migrate to the surface at night, is important for White-tailed Tropicbirds throughout the world. Indeed, of the 14 regurgitations and prey remains obtained at nests in 2001 and 2002 on Aride, 30% had squid. Other important prey items were flying fish (Exocoetidae) and mullids (Mullidae), suggesting that prey also were captured during the day. Presumably the Aride birds foraged closer to their breeding grounds than the Caribbean birds because coastal species such as mullids were not found in the diet of Puerto Rican birds (F. C. Schaffner pers. comm.).

We found significant relationships between chick provisioning and day, nest, and year. Daily variation in chick food provisioning was rather small, i.e., it was due to an effect of meal size received on 3 of 60 days in 2001. Chick feeding frequency of surviving chicks was significantly higher in 2001 than in 2002, suggesting that food availability was higher in 2001. In fact, productivity (number of chicks fledged per pair) was slightly higher in 2001 (0.29, n = 68) than in 2002 (0.27, n = 42; unpubl. data). While surviving chicks in 2001 received food more frequently than did surviving chicks in 2002, NET values did not differ significantly between years. Presumably, lighter chicks were less costly to maintain, reduced their activity (Schreiber 1994), and/or their metabolic rates were adjusted to lower food delivery rates (Klaassen and Bech 1992). The ability to grow more slowly as a response to lowered food provisioning, and still survive, has important advantages for species, such as the White-tailed Tropicbird, that are subjected to a high degree of variability and unpredictability in collecting food resources (Navarro 1992, Schreiber 1994). However, within each age class in 2001, the NET values of surviving chicks were similar

to those of nonsurviving chicks. This suggests that underweight chicks reduced their growth to a very large extent, with a presumed progressively reduced metabolism and body temperature (Klaassen and Bech 1992), and perish only after a prolonged period of low food delivery.

The difference in food delivery to surviving chicks between years occurred at the level of feeding frequency rather than meal size. Granadeiro et al. (1998), studying Cory's Shearwater (*Calonectris diomedea*) in the Atlantic Ocean, reached a similar conclusion. Annual differences in feeding frequency, but not in meal size, seem to be a widespread phenomenon in seabirds. Energetic constraints should impose a strong selection for parents to increase the individual meal size, while reducing the number of feedings as much as possible (Schaffner 1990). Direct observations of individually marked White-tailed Tropicbird adults showed that the typical payload size carried by adults was significantly less than half of the size that they can transport. The chicks' swallowing capabilities occur before the parents' transport limits are reached, and seem to set the load carried by individual parents at a size that they can easily transport (about 40% of the maximum payload size; Schaffner 1990). Due to great spatial and temporal variation in the food supply, it is expected that feeding frequency will show greater variability than meal size (Schaffner 1990), which is what we found in our comparison between years and between surviving and nonsurviving chicks. Red-tailed Tropicbirds breeding on Johnston Atoll, central Pacific Ocean, also showed a greater variability between years in feeding frequency than in meal size (Schreiber 1994).

The low abundance and unpredictability of food resources in tropical areas often has been suggested as a reason for lower seabird productivity in the tropics (Ashmole 1963, Ramos 2000). The differences in feeding frequency and meal size between surviving and nonsurviving White-tailed Tropicbird chicks, and the lesser importance of daily variation in meal size, suggest that within a particular year, even good feeding conditions cannot mask the effect of optimal feeding frequency by parents.

Chick food provisioning: comparison with other pelagic seabirds.—Results from other studies of pelagic seabirds are similar to our results in showing smaller meals and a higher feeding frequency for very young chicks than for older chicks (Schreiber 1994, Bolton 1995, Hamer and Hill 1997, Ramos et al. 2003). Such general trends should result from a gradual increase in the overall capacity of the digestive tract (Phillips and Hamer 2000) and the swallowing capacity of chicks (Schaffner 1990). In agreement with studies of Red-tailed Tropicbirds (Schreiber 1994) and other pelagic seabirds (e.g., procellariiforms; Bolton 1995, Ramos et al. 2003), the increased demand in food requirements as chicks grew was paralleled by an increase in the amount of food consumed (for chicks aged up to 50 days in our study), but not in the daily feeding frequency. For surviving chicks of White-tailed Tropicbirds the percentage of days that chicks were fed showed little age-specific variation until chicks reached the oldest age class. Also, Schreiber (1994) observed Red-tailed Tropicbird chicks from dawn to dusk, and found that the number of feedings received per day by medium and large chicks was similar. An increase in the daily amount of food received by White-tailed Tropicbird chicks as they grew can be explained by an increase in the swallowing capacity of chicks, the meal delivery frequency of parents, and the probability of both parents returning to the nest simultaneously (the chick receives the entire meal size or none of it; thus, if both parents arrive at approximately the same time with a combined amount of food larger than the chick's swallowing capacity, the second meal will be completely lost). Tropicbirds feed their chicks with meals consisting of a combination of large and small items (Schaffner 1990, JAR pers. obs.), and the risk of wasting oversized meals is much higher than in seabirds that feed their chicks with partially digested food or with stomach oil of high calorific content (e.g., procellariforms; Phillips and Hamer 2000).

In situations of low resource availability, temperate procellariiforms deliver larger meals at a lower feeding frequency than those delivered under favorable feeding conditions (Chaurand and Weimerskirch 1994, Granadeiro et al. 1998), presumably as a compromise between feeding their chicks and maintaining their own body condition (Weimerskirch et al.

1997). We did not find evidence of this mitigating feeding behavior in White-tailed Tropicbirds because in 2002, when food presumably was less abundant than in 2001, the adults decreased the feeding frequency but did not increase the size of the meals delivered to chicks. Increasing meal size may not be an option for tropical seabirds that feed on dispersed prey such as flying fish.

Natural selection has produced White-tailed Tropicbird parents that carry an approximately optimal payload size to their chicks, imposed by mechanical and volume constraints (of which the maximum swallowing capacity of chicks is the most important) and energetic constraints such as weather, food abundance and availability, and distance of food sources from the nesting colony (Schaffner 1990). Such selection pressures seem to have fixed the meal mass at a relatively narrow size, that the adults will try to collect as quickly as possible (Schaffner 1990). Our study shows that (1) individuals vary in their abilities to provide optimal provisioning to their chicks (which is related to chick survival), and (2) environmental conditions (shown by our differences in feeding frequency between years) provide important energetic constraints for parents in provisioning their chicks. Changes in the abundance and availability of food resources due to anthropogenic influences are likely to affect the optimal provisioning of chicks, with possible negative consequences on the survival of White-tailed Tropicbird nestlings.

Although food delivery varied between years, we were unable to determine if low chick provisioning affected the entire population, and thus could account for the decline of the White-tailed Tropicbird population on Aride Island (Bowler et al. 2002). However, as White-tailed Tropicbirds breed throughout the year, chick food provisioning also should be examined during the northwest monsoon season (October to April).

ACKNOWLEDGMENTS

LITERATURE CITED

ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

BOLTON, M. 1995. Food delivery to nestling storm petrels: limitation or regulation. Funct. Ecol. 9:161–170.

BOWLER, J., M. BETTS, I. BULLOCK, AND J. A. RAMOS. 2002. Seabird population trends on Aride Island Nature Reserve, Seychelles 1988–2000. Waterbirds 25:285–294.

CHAURAND, T. AND H. WEIMERSKIRCH. 1994. The regular alternation of short and long trips in the Blue Petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. J. Anim. Ecol. 63:275–282.

GRANADEIRO, J. P., M. NUNES, M. C. SILVA, AND R. W. FURNESS. 1998. Flexible foraging strategy of Cory's Shearwater during the chick-rearing period. Anim. Behav. 56:1169–1176.

HAMER, K. C. AND J. K. HILL. 1997. Provisioning and growth rates of nestling Fulmars *Fulmarus glacialis*: stochastic variation or regulation? Ibis 139:31–39.

HUIN, N., P. A. PRINCE, AND D. R. BRIGGS. 2000. Chick provisioning rates and growth in Black-browed Albatross *Diomedea melanophris* and Grey-headed Albatross *D. chrysostoma* at Bird Island, South Georgia. Ibis 142:550–565.

KLAASSEN, M. AND C. BECH. 1992. Resting and peak metabolic rates of Arctic Tern nestlings and their relations to growth rate. Physiol. Zool. 65:803–814.

LACK, D. 1966. Population studies of birds. Oxford Univ. Press, Oxford, United Kingdom.

NAVARRO, R. A. 1992. Body composition, fat reserves, and fasting capability of Cape Gannet chicks. Wilson Bull. 104:644–655.

PHILLIPS, N. J. 1987. The breeding biology of White-tailed Tropicbirds *Phaethon lepturus* at Cousin Island, Seychelles. Ibis 129:10–24.

PHILLIPS, R. A. AND K. C. HAMER. 2000. Growth and provisioning strategies of Northern Fulmars *Fulmarus glacialis*. Ibis 142:435–445.

PRYS-JONES, R. P. AND C. PEET. 1980. Breeding periodicity, nesting success and nest site selection among Red-tailed Tropicbirds *Phaethon rubricauda* and White-tailed Tropicbirds *P. lepturus* on Aldabra Atoll. Ibis 122:76–81.

RAMOS, J. A. 2000. Characteristics of foraging habitats and chick food provisioning by tropical Roseate Terns. Condor 102:795–803.

RAMOS, J. A., A. M. MAUL, V. AYRTON, J. HUNTER, J. BOWLER, I. BULLOCK, G. CASTLE, R. MILETO, R. LIDSTONE-SCOTT, P. LIDSTONE-SCOTT, AND C. PACHECO. 2002. The influence of oceanographic conditions and timing of breeding on tropical Roseate Tern reproductive parameters. Mar. Ecol. Prog. Ser. 243:271–279.

RAMOS, J. A., Z. MONIZ, E. SOLA, AND L. R. MONTEIRO. 2003. Reproductive measures and chick growth of Cory's Shearwater (*Calonectris diomedea borealis*) in the Azores. Bird Study 50:47–54.

RICKLEFS, R. E. 1984. Meal sizes and feeding rates of Christmas Shearwaters and Phoenix Petrels on Christmas Island, Central Pacific Ocean. Ornis Scand. 15:16–22.

RICKLEFS, R. E., C. H. DAY, C. E. HUNTINGTON, AND J. B. WILLIAMS. 1985. Variability in feeding rate and meal size of Leach's Storm-Petrel at Kent Island, New Brunswick. J. Anim. Ecol. 54:883–898.

SCHAFFNER, F. C. 1990. Food provisioning by White-tailed Tropicbirds: effects on the developmental pattern of chicks. Ecology 71:375–390.

SCHREIBER, E. A. 1994. El Niño-Southern Oscillation effects on chick provisioning and growth in Red-tailed Tropicbirds. Col. Waterbirds 17:105–119.

SCHREIBER, E. A. 1996. Experimental manipulation of feeding in Red-tailed Tropicbird chicks. Col. Waterbirds 19:45–55.

SCHREIBER, E. A. 2002. Climate and weather effects on seabirds. Pp. 179–215 *in* Biology of marine birds (E. A. Shreiber and J. Burger, Eds.). CRC Press, Boca Raton, Florida.

STONEHOUSE, B. 1962. The tropicbirds (genus *Phaethon*) of Ascension Island. Ibis 103:123–161.

WARHAM, J. 1990. The petrels: their ecology and breeding systems. Academic Press, London, United Kingdom.

WEIMERSKIRCH, H., Y. CHEREL, F. CUENOT-CHAILLET, AND V. RIDOUX. 1997. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. Ecology 78:2051–2063.

ZAR, J. H. 1996. Biostatistical analysis. Prentice-Hall International, London, United Kingdom.